# ON THE METHOD OF FEEDING OF FOUR PELECYPODS

G. E. MACGINITIE

(*From the William G. Kerckhoff Marine Laboratory of the California Institute of Technology, Corona del Mar, California*)

## Introduction

The feeding tracts of many pelecypods have been described, but while many of these accounts have approximated the true conditions, there is one important fact that has been omitted, and it is upon this that an understanding of their feeding methods depends.

When the pelecypods used in this experiment were feeding, a sheet of mucus entirely covered the gill structure, and it is this mucous sheet which strains out food material from the water vascular current. Cilia serve only to create the current and move the mucus. With the exception of highly specialized or quite primitive forms, it is probable that this method of feeding is general in the class Pelecypoda.

Except in cases where the animal has been left sufficiently long (usually long enough to begin the regeneration of the shell and mantle), a pelecypod which has been cut open is not feeding. When disturbed, the pelecypods that I have investigated cease feeding at once, and, when brought into the laboratory, several days may elapse before they will feed naturally. Therefore, it is necessary to make certain that the animal which is being investigated is adjusted to its surroundings and is carrying on its activities exactly as though it were in its natural habitat. Many pelecypods will begin feeding shortly after being brought into the laboratory, provided they are not mutilated in any way. In such cases feeding may begin within a few hours, and, in time, these animals actually become somewhat adapted to oft repeated disturbances.

## Materials and Methods

Four pelecypods were used, namely, the gaper clam, *Schizothaerus nuttallii;* the mud flat scallop, *Pecten circularis;* the native West Coast oyster, *Ostrea lurida;* and the West Coast mussel, *Mytilus californianus.* These represent a burowing form, a surface form, an above surface form, and an open coast form. The first three use detritus for food, and the fourth uses plankton.

A hole was bored in different positions in one side of the shell of different individuals of each species, so that ultimately all regions connected with the feeding activities of each of these pelecypods could be observed. These windows were covered with a thin piece of glass, the size of the window depending upon what region and how much area of the region was to be investigated.

The openings were made by grinding a portion of the shell away, removing the underlying mantle, and then cementing a piece of cover-glass over the hole. The cover-glass was cut to shape by means of carborundum points and cemented in place with United Mender. Many cements were used, but the United Mender made by the United Sales Co. of New York, Dallas and Los Angeles proved to be by far the best; for windows cemented in place with it remained in place for as long as six months, although they were continuously immersed in ocean water. Before the cement was applied both the cover-glass and the rim of the shell around the opening were wiped clean with a clean cloth dampened with 95 per cent alcohol.

It is necessary to have the shell surrounding the opening perfectly flat before the cover-glass is cemented in place. A sander grinds faster and generates less heat than an emery wheel. While one is grinding the opening the animal should be dipped often into ocean water. A small hand rotor and dentist's drills can be used to advantage to cut the opening, and then only the surface surrounding the opening need be sanded flat.

A binocular and microscope lamp were suitably mounted next the aquarium in such a manner that they could be adjusted to any position.

After a window was put in a shell the animal was left undistturbed in running sea water for about two weeks, then watched carefully through the windows with the binocular to determine if feeding was being carried on in a natural manner. This was determined by introducing into the water some non-irritating material which constitutes the natural food of the animal.

The food material used was either a diatom culture or detritus, the latter being preferable. When the surface of the mud of an estuary or of the ocean is disturbed, a grayish turbidity results. The material causing this turbidity consists of decaying organic matter which is rich in bacteria, protozoa and other organisms such as rhabdocoeles, nematode worms, larvae of many species of marine animals, and, in addition, on mud flats there are usually surface diatoms and single-celled algae. This surface sediment or detritus, which constitutes the main, or, in many cases, the only source of food for burrowing or surface pelecypods, is obtainable in any quantity and is readily eaten by most pelecypods. When introduced as food it does not disturb the feeding activities of the clams. (A diatom culture was found to be better for *Mytilus californianus.*)

## FEEDING

In the four species listed above, when feeding begins either mucus is secreted at the upper edges of the gills and is carried in a sheet by the frontal cilia to the free edges of the gills, or it is secreted more or less uniformly over the entire surface. It is then carried in strings along the edges of the gills to the labial palps. The palps perform a selective function, at least to the extent of partially removing undesirable particles, while allowing the rest of the material to pass intact with the strings of mucus directly into the esophagus in the form of food-laden strings of mucus. The main point to be stressed here is that the sheet of mucus covers the entire gill in much the same manner as described for tunicates (MacGinitie, 1939), and intercepts all particles from the current of water which passes through the gills and out through the dorsal or excurrent channels.

I consider a pelecypod to be feeding when a sheet of mucus entirely covers the gills, at which times all particles in the water, however small they may be, are strained out by the mucus. I am referring to undisturbed animals. Mucus may be made to flow copiously from any portion of a gill by direct stimulation, but it is very difficult to determine just where and when the secretion of mucus for feeding takes place. For this reason it took more than two years of careful observation to be sure of the main points set forth in this paper. Since mucus itself is perfectly transparent, the presence of the sheet of mucus is shown only by the included detritus. When feeding is actually going on, as witnessed through a window in the shell, the sheet of mucus may not follow the grooves, but, as shown by particles in it, may be deflected somewhat in an anterior direction, the particles carried by it crossing over the grooves, for they are carried by the mucus and not by the cilia. For example, when the mucus sheet is present in *Mytilus californianus,* the pull of the cilia of the free edge of the gills causes the sheet to be deflected ahead, particularly near the lower edge of the gills. Thus it is seen that the sheet of mucus, and not the cilia, carries the food particles.

When particles are moved by the cilia in the absence of the mucous sheet, as in the case of an opened clam when one valve and mantle have been removed, such particles follow the grooves. As it is the frontal cilia which move the mucus, it is to be expected that when the mucous sheet is absent, that is, when feeding is not taking place, the particles being moved to the free edge of the gills will move parallel to the grooves. The current of water created by the lateral cilia bordering the grooves tends to hold the particles in the grooves as they are being moved by the frontal cilia towards the free edges of the gills. In some pelecypods particles will move both down the ridges and up the grooves. The ciliary mechanisms have been worked out in great detail by Atkins (1936, 1937, 1938).

When a small amount of carmine powder is mixed with the detritus and introduced with the incurrent water, it is usually ingested. In *Mytilus californianus* and *Schizothaerus nuttallii* if carmine alone is introduced in the same manner, some of it will find lodgment on the sheet of mucus already formed; but the sheet nearly always will be cut off at the upper edge and the carmine which thereafter collects on the gills will be carried down the grooves, thence forward along the edge of the gill, and then dropped by the labial palps into the anterior portion of the mantle cavity. In *Mytilus californianus* rejected material that is dropped into the anterior portion of the mantle cavity is carried posteriorly by grooves just within the mantle edge and issues from the posterior end in a continuous string termed pseudofeces. I have carefully observed, through windows at the anterior portion of several *Mytilus californianus,* the rejection of the undesirable material by the labial palps. The palps spread apart and assume a transverse position. The mucous threads from the edges of the gills travel directly to the bases of the ventral palps, down their anterior edges and thence into the ventral grooves of the mantle edge, where the laden threads of mucus travel to the posterior end and out as the pseudofeces mentioned above. When *Mytilus californianus* is feeding, the palps are laid backward outside of and close to the gills.

In *Schizothaerus nuttallii* rejected material will be forcibly ejected from the mantle cavity by a sharp contraction of the adductor muscles, which quickly brings the valves together and squirts the water and rejected material from the mantle cavity out through the incurrent siphon or opening.

This activity undoubtedly accounts for some of the squirting by clams on mud flats when the tide is going out. As the tide is leaving the mud flats, clams that have long siphons and burrow deeply squirt much more often than they do when the tide is in and they are covered by water. When the mud flats are nearly bare a considerable amount of sand and other undesirable material stirred up by the action of the waves may cause material that will be rejected to accumulate rather rapidly. Long-necked clams usually eject water much more forcibly than do those clams which live much nearer the surface. *Schizothaerus nuttallii* squirts water to a height of from 3 to 5 feet. Such removal of rejected material, or squirting, is also much more frequent when the tide is first coming in, as will be evident to anyone who will take the trouble to stand knee deep in the incoming tide in a clam bed and observe.

The mantle cavities of the four pelecypods were never free of mucus, and particles are at all times conveyed to and along the edges of the gills by mucus, but it is only at feeding times that the gills are covered by the sheets of mucus. While feeding is going on these sheets are being continuously secreted and move slowly toward the free edges of the gills.

It should be noted here that some mucus with its included particles may find its way into the mouth when the sheet of mucus is not present. I think this is sometimes due to testing the mucus for suitable food, for the secretion of the mucous plate often follows such testing. Abnormal ingestion of material often follows disturbance or mutilation. This is clearly shown by placing carmine or carborundum on the gills of a pelecypod which has been opened. Under such conditions the introduced material may be carried to the mouth and ingested. This never happens in the case of a pelecypod which is feeding normally in an aquarium as observed through a window, for the introduction of even small amounts of carmine or carborundum causes the pelecypod to cease feeding immediately. I consider carborundum particles the most undesirable of all materials to use in feeding experiments.

In connection with the above, I am of the opinion that the function of the osphradia as "water testing organs" is over-emphasized in the pelecypods. The region which seems to me to have the highest tactile and "olfactory" sense is the region where the incurrent opening is located. In *Mytilus, Pecten* and *Ostrea* it is the edge of the mantle; in *Schizothaerus* it is the finger-like papillae which partially close the entrance of the incurrent siphon and act as a coarse strainer. When a valve has been removed, part of the reception area for stimuli has been removed, and the nervous system of the pelecypod is rather badly upset, to say the least. What an animal does with the mucous threads from its gills at such a time had better be disregarded.

## Discussion

It is unwise to speak of feeding in a pelecypod unless it is actually observed doing so. Pelecypods are very sensitive to stimulation, either mechanical or chemical (Hopkins, 1932*a*, 1932*b*), and sometimes will cease feeding at the least movement or change in food material. In general, I think it may be said that small or juvenile members of any species are less sensitive than the older and larger ones, for they adjust themselves more quickly to handling and begin feeding sooner after the window is placed in them. For this reason it is best to use as young specimens as one can conveniently. They are quite erratic for several days after being moved into the laboratory, and also after any major disturbance. However, when once fixed and left alone for a considerable length of time, which varies in each individual, they become much more uniform in their feeding activities, although apparently none of them ever feed continually. The rate of intake of water varies considerably, and this is usually or perhaps always accompanied by some contraction of the gills. Complete contraction of the gills shuts off the current of water entirely, just as a similar contraction does in the tunicate basket (MacGinitie, 1939). It is impossible for large particles to pass through the gills. Whether such small particles as bacteria pass through or not depends on whether or not the pelecypod is feeding.

It is well known that cilia often have a selective function, fine examples being the cilia of the pouch and funnel of *Stentor* (Schaeffer, 1910), and the egg and sperm collectors of *Urechis* (MacGinitie, 1935). Nevertheless, the separation of solid material from water currents is much more efficiently done by straining such water through mucus. It is not surprising, therefore, that mucus plays a much more important rôle in the feeding mechanisms of plankton and detritus feeders than it has been given credit for doing. Certainly it never should be said that a pelecypod is feeding just because it is pumping or maintaining a current through the mantle cavity.

In the light of the information presented here, it is interesting to read other papers concerned with the feeding of pelecypods and even certain gastropods (Orton, 1912). When the use of a mucous sheet for straining food material from the water is understood it will eliminate many points of discussion that have arisen. Although many papers concerned with the feeding of pelecypods have been written, only a few are listed in this paper, for the literature on this subject is rather voluminous. Therefore, the reader is referred to the following papers for complete bibliographies on the subject (Atkins, 1936–38; Galtsoff, 1928; Hopkins, 1936; Nelson, 1938; Orton, 1912; Yonge, 1936; and ZoBell and Feltham, 1938).

When it is understood that the food material of pelecypods in general is strained from the water as it passes through a sheet of mucus, and that feeding is being carried on only when such a sheet is present, it will clear up practically all points of uncertainty that one meets in reading about feeding methods and feeding experiments in the pelecypod mollusks.

## Summary

1. Openings were made through the valve and mantle of four species of pelecypods. These were made in various positions in the valves of many individuals so that ultimately all outer portions of the feeding mechanisms could be observed. These openings were covered with pieces of cover-glass cemented in place so as to form windows through which the feeding activities could be watched.

2. The feeding activities were observed through a binocular without in any way disturbing the animals.

3. Evidence is given to show that when a pelecypod is feeding a sheet of mucus covers the gills, and it is this mucus which strains the food material from the water, the cilia affording mechanical means for its transportation.

4. While the pelecypod is feeding this mucus is constantly being secreted and is carried to the food grooves bordering the gills, along which it is transported to the mouth as strings of food-laden mucus.

## LITERATURE CITED

Atkins, Daphne, 1936. On the ciliary mechanisms and interrelationships of lamellibranchs. Part I. Some new observations on sorting mechanisms. *Quart. Jour. Micr. Sci.,* **79**: 181–308.

Atkins, Daphne, 1937*a*. On the ciliary mechanisms and interrelationships of lamellibranchs. Part II. Sorting devices on the gills. *Quart. Jour. Micr. Sci.,* **79**: 339–373.

Atkins, Daphne, 1937*b*. On the ciliary mechanisms and interrelationships of lamellibranchs. Part III. Types of lamellibranch gills and their food currents. *Quart. Jour. Micr. Sci.,* **79**: 375–421.

Atkins, Daphne, 1937*c*. On the ciliary mechanisms and interrelationships of lamellibranchs. Part IV. Cuticular fusion, with special reference to the fourth aperture in certain lamellibranchs. *Quart. Jour. Micr. Sci.,* **79**: 423–445.

Atkins, Daphne, 1938. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VII. Latero-frontal cilia of the gill filaments and their phylogenetic value. *Quart. Jour. Micr. Sci.,* **80**: 345–436.

Galtsoff, Paul S., 1928. Experimental study of the function of the oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. *Bull. Bur. Fish.,* **44**: 1–39.

Hopkins, A. E., 1932*a*. Sensory stimulation of the oyster, Ostrea virginica, by chemicals. *Bull. Bur. Fish.,* **47**: 249–261.

Hopkins, A. E., 1932*b*. Chemical stimulation by salts in the oyster, Ostrea virginica. *Jour. Expcr. Zool.,* **61**: 14–28.

Hopkins, A. E., 1936. Adaptation of the feeding mechanism of the oyster (Ostrea gigas) to changes in salinity. *Bull. Bur. Fish.,* **48**: 345–364.

MacGinitie, G. E., 1935. Normal functioning and experimental behavior of the egg and sperm collectors of the echiuroid, Urechis caupo. *Jour. Expcr. Zool.,* **70**: 341–354.

MacGinitie, G. E., 1939. The method of feeding of tunicates. *Biol. Bull.,* **77**: 443–447.

NELSON, THURLOW C., 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of Ostrea virginica, O. edulis and O. angulata, with comparisons with other species of the genus. *Jour. Morph.*, **63**: 1–61.

ORTON, J. H., 1912. The mode of feeding of Crepidula, with an account of the current-producing mechanism in the mantle cavity, and some remarks on the mode of feeding in gastropods and lamellibranchs. *Jour. Mar. Biol. Assoc.*, N. S., **9**: 444–478.

SCHAEFFER, ASA ARTHUR, 1910. Selection of food in Stentor coeruleus. *Jour. Exper. Zool.*, **8**: 75–132.

YONGE, C. M., 1936. Mode of life, feeding, digestion and symbiosis with Zooxanthellae in the Tridacnidae. *Scientific Reports Great Barrier Reef Exp.* 1928–29, **1**: 283–321.

ZOBELL, CLAUDE E., AND CATHARINE B. FELTHAM, 1937–1938. Bacteria as food for certain marine invertebrates. *Sears Found. Jour. Mar. Res.*, **1**: 312–327.